ALTERNATION OF GENERATIONS IN THE ROTIFER *LECANE INERMIS* BRYCE

I. Life Histories of the Sexual and Non-sexual Generations

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Contents

The Organism

The small loricate rotifer, *Lecane* (*Distyla*) *inermis* Bryce, presents many advantages for the study of the alternation of parthenogenetic and bisexual generations, common among the rotifers, and of the life histories of the diverse types of individuals that occur. It is hardy, easily cultivated, multiplies rapidly and changes readily from the non-sexual to the sexual condition and vice versa. The entire life of the female lasts usually but nine or ten days, and the first offspring appear on the second or third day. This organism is of interest as a representative of a genus in which the occurrence of males has not

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hitherto been described (Wesenberg-Lund, 1930, p. 94). The male of this species was first observed by Finesinger subsequent to his study (1926) of the inheritance of certain environmental effects in a succession of generations of parthenogenetic females.

Lecane inermis is one of the slow-moving rotifers, common in wet sphagnum. It belongs to the family Euchlanidæ, which is characterized by the possession of a lorica composed of two parts, a dorsal and a ventral plate, connected by lateral sulci. In *Lecane inermis* the lorica is extremely flexible, so that dorsal and ventral plates are barely distinguishable; the animal therefore resembles somewhat the more primitive, soft-bodied notommatids, with which the euchlanids are classified by Wesenberg-Lund (1929). A full description of this and other species of *Lecane* is given by Harring and Myers (1926). The individuals (females) of the stock employed in the present investigation are somewhat larger than the dimensions given for this species by Harring and Myers. Adults are 175–190 μ in length by 65–75 μ in breadth; newly-hatched individuals are about 130 μ in length by 33 μ in breadth.

As is well known, the rotifers of most common occurrence are the parthenogenetic or amictic females, and specific descriptions are based, in large measure, on these. In a single species there may occur, however, three sorts of individuals: the common amictic or non-sexual females, the mictic or sexual females, and the males. An outline of the change of generations will facilitate the understanding of the present study.

Outline of the Change of Generations

(Compare Fig. 1)

The common non-sexual or amictic females (*A*) multiply exclusively by parthenogenesis. They deposit eggs (*f*) that are ellipsoid in form, with a thin, smooth, outer membrane. These eggs carry the diploid number of chromosomes, are incapable of fertilization and produce females, usually like the mother, so that multiplication by (diploid) parthenogenesis may continue for many generations. But among the females produced by such eggs are at times individuals (*M*) that bring forth small eggs (*m*) which develop into the small, male individuals. These females are called mictic because their eggs are capable of being fertilized. They resemble outwardly the amictic females. The small, male-producing eggs carry the haploid number of chromosomes. There is some evidence that the male embryo may either double its chromosomes during development (*Asplanchna intermedia*, Tauson, 1924) or develop entirely with the haploid number (*Asplanchna amphora*, Whitney, 1929). When the mictic females are fertilized they produce, instead of the small, haploid, male-producing eggs, larger, dark eggs with a thick, horny shell. Such an egg has, of course, the diploid number of chromosomes. It remains unhatched for some time, and then produces a parthenogenetic or amictic female,

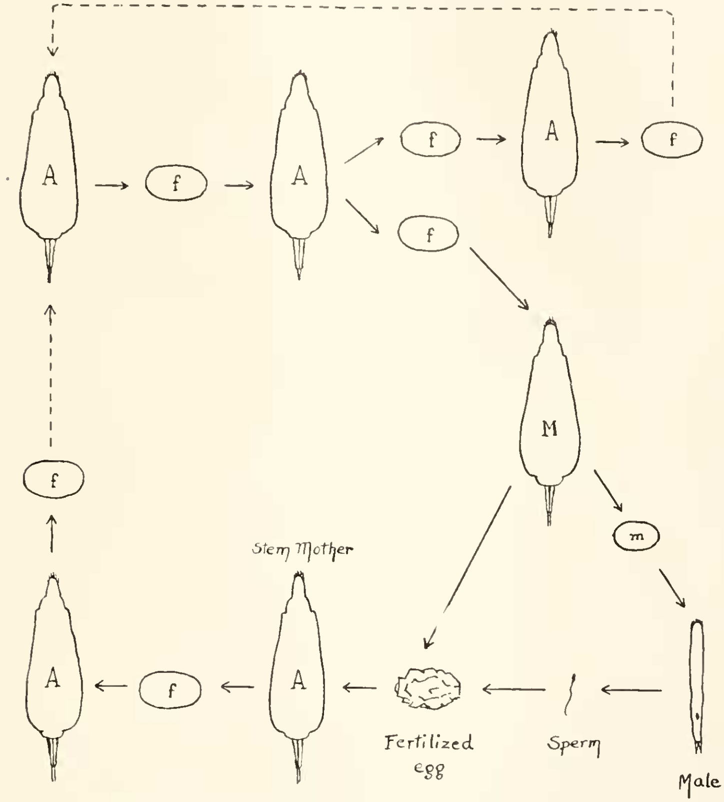


FIG. 1. Diagram showing the alternation of sexual and non-sexual generations in a bisexual rotifer, such as *Lecane inermis*. The most common type of individual, the non-sexual "amictic" female (*A*), reproduces exclusively by diploid parthenogenesis. Its eggs (*f*) develop invariably into females, which are usually amictic, so that multiplication by diploid parthenogenesis may continue for many generations (as indicated by the long, broken-lined arrows). But the daughters of the amictic female may be "mictic" (*M*). Their eggs are haploid, and develop parthenogenetically (*m*) into males, or, if fertilized, produce non-sexual amictic females, the "stem mothers," with which the cycle begins anew.

with the diploid number of chromosomes. From such a female, commonly spoken of as the stem mother, begins again the cycle of diverse generations just described.

The purpose of the present investigation is to analyse this cycle in the species *Lecane inermis;* to give an account of the different types of individuals composing it, and to discover the factors that cause their production. This first paper presents a description of the different types of individuals, with a comparative study of their life histories. A later paper, now in preparation, will deal with the factors causing the change of generations.

Culture Methods

Lecane inermis is readily cultivated in grain infusions of proper strength, in malted milk, and in some standard inorganic culture media to which are added suitable food organisms. Oat infusion, used by Jennings and Lynch (1928—I) for *Proales sordida*, is (as they observe) a satisfactory medium also for *Lecane inermis*. An infusion of suitable strength is prepared by boiling twenty flakes of rolled oats for three minutes in 100 cc. of spring water, filtering while hot, and allowing to stand 24 hours before using. This "standard" oat infusion was employed in the comparative studies of the life histories of the different types of individuals and in the early part of the experimental work.

For precise experimental study of the influence of the environment on the kinds of individuals that occur, a more exactly controllable culture medium is necessary. Luntz (1926, 1929) has demonstrated the usefulness of synthetic inorganic media, such as the Benecke and Knop solutions, in the experimental investigation of the life cycle of rotifers. The food is controlled by the use of pure strains of food organisms, and the pH and initial salt concentration are likewise under control.

Benecke's solution in 0.07 per cent concentration, with addition of suitable food organisms, provides a most satisfactory culture medium for *Lecane inermis*. To it were added pure strains of certain bacteria, *B. proteus*, *B. subtilis* and *B. coli* (obtained from the School of Hygiene of the Johns Hopkins University). Such pure strains are inadequate as food, the rotifers surviving in them for but three generations. A mixture of two or three of these strains of bacteria is more satisfactory. Addition of green algæ to the bacteria gives still better results. A number of different algæ, obtained from the laboratory of Pringsheim at Prague, were tested. Species of *Chlamydomonas* and *Euglena* were apparently too large to serve as food for *Lecane inermis*. *Chlorella vulgaris* Beyerinck proved to be suitable, particularly when combined with *B. proteus*. The mixture of *Chlorella* and *B. proteus* has been employed in much of the experimental work. *Chlorella* is grown on beef agar, *B. proteus* on bacteriological agar.

A fresh suspension of these two food organisms in the culture solution is prepared daily immediately before the transfer of the rotifers.

In order to avoid contamination with other organisms, bacteriological precautions are observed in the preparation of the culture medium and food suspension, and in the handling of the rotifers. The method is, with a few necessary alterations, that devised by Raffel (1930) for the culture of *Paramecium*. The rotifers are cultivated individually on hollow-ground slides, placed in sterile Petri dishes containing distilled water. They are transferred daily with sterile, cotton-stoppered pipettes. A fuller account of the method of culture will be given in a later paper on the factors causing the change of generations.

Life Histories of the Diverse Types of Individuals

Knowledge of the general biology of the bisexual generations of rotifers is not extensive. This is doubtless due in part to the rare occurrence of sexual individuals in many of the species that have been employed for laboratory investigations. There have been few detailed comparative studies of the lives and activities of the mictic and amictic females, though such studies are much needed for an understanding of the fundamental difference between them, and of the different rôles they play in the life history of the species. Knowledge of the life history of the males is in little better case. *Lecane inermis* is a favorable organism for supplying these needs, since it readily yields an abundance of all types of individuals.

The Amictic and the Unfertilized Mictic Females: Comparison

The amictic and mictic females of *Lecane inermis* resemble each other closely, but differ markedly in certain features of their life histories, particularly in fecundity and length of life.

The mature females, whether amictic or mictic, present the appearance shown in Fig. 2.

As in *Proales sordida* (Jennings and Lynch, 1928—I), four periods may be distinguished in the life of the individual: (1) The period of embryonic development, from the deposition of the egg to hatching; this requires, in *Lecane inermis*, about one and one-half days. (2) The immature period, one of rapid growth and activity, concluding as a rule on the third day with the deposition of the first egg. (3) The period of fecundity, five or six days during which the eggs one at a time are matured and deposited in regular succession. (4) The post-fecund period, or period of old age, during which the activities of the female gradually cease, structural degeneration sets in and death ensues, usually on the ninth day, though it may be deferred for varying periods, depending on the conditions.

The amictic female.—The term *amictic* was first applied by Storch (1924) to the commonest type of rotifer female, since it cannot reproduce by amphimixis. The cytological investigations by Whitney, Storch, Nachtwey and others, of several species of rotifers, have shown that the eggs of the amictic female invariably develop by diploid parthenogenesis and produce diploid females, which may be either amictic or mictic.

The amictic females of *Lecane inermis* produce eggs that are ellipsoid in form and measure about 64 μ by 38 μ (Fig. 6). They are covered with a thin membrane surrounded by a gelatinous layer which swells, separates from the egg and disappears before the embryo emerges, about 30 hours after deposition.

The mictic female is capable of reproduction by amphimixis. Its eggs, as shown by the above-mentioned investigators, undergo reduction in the number of chromosomes. The mictic female of *Lecane inermis*, although indistinguishable in appearance from the amictic female, is immediately recognizable by the kinds of eggs it produces.

EXPLANATION OF PLATE

These drawings were reconstructed from many camera lucida sketches, for which a Zeiss microscope was used with oc.15x, obj.8.3, and with oc.15x, (Leitz) obj.3. The magnification of the seven figures is 518 diameters; this magnification was obtained by doubling the average dimensions of sketches of eggs and of living individuals, made with oc.15x, (Leitz) obj.3.

Abbreviations

c, contractile vacuole
d, rudiment of anterior portion of the digestive system
g, gastric glands
ex, excretory (?) granules
i, intestine
m, mastax
p.g., prostate (?) glands
o, ovary
oe, œsophagus
r, retro-cerebral organ
t, toes
te, testis
v.d., vas deferens

FIG. 2. Mature female (mictic or amictic); dorsal view.

FIG. 3. Young female, shortly after hatching; lateral view, showing prominent mastax, gastric glands, œsophagus, intestine and contractile vacuole.

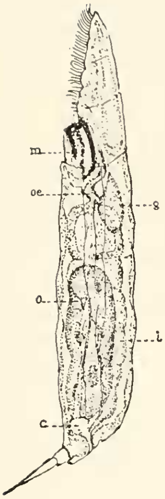
FIG. 4. Male; dorsal view.

FIG. 5. Male; lateral view, for comparison especially with Fig. 3. The digestive system is represented only by an anterior rudiment; the contractile vacuole is absent.

FIG. 6. The (female-producing) egg of the amictic female, several hours after deposition; lateral view. The gelatinous layer has separated from the egg membrane.

FIG. 7. The (male-producing) egg of the mictic female, before the initiation of cleavage.

FIG. 8. The fertilized (female-producing) egg of the mictic female.



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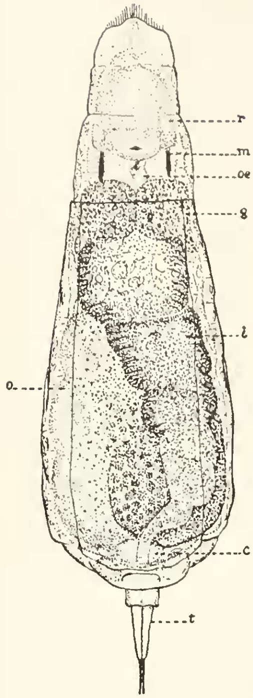

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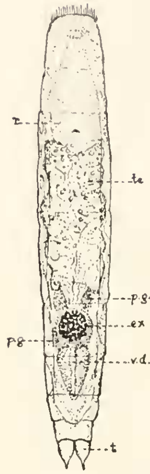

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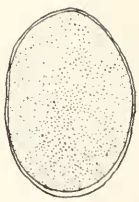

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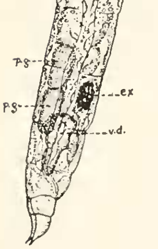

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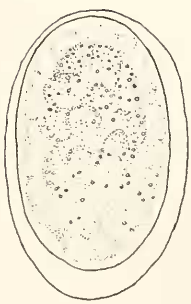

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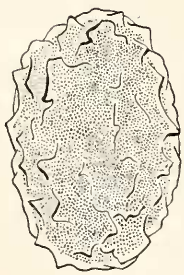

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If unfertilized, the eggs (Fig. 7) resemble the female parthenogenetic eggs, except that they are smaller (44 μ by 32 μ) and produce males.

The fertilized eggs (Fig. 8) are larger (64 μ by 38 μ), covered with a thick, horny shell, and produce amictic females. They are very black when laid, but the color fades to light brown in the course of several days. In this condition they remain for a period varying from a few days to two months. They withstand drying, which does not seem to alter their hatchability. Ordinarily, only 20 per cent to 30 per cent hatch in spring water or in oat infusion. Further investigation of the hatchability of the fertilized eggs is much needed. The course of development of these eggs has not been studied in detail. Apparently, cleavage begins shortly after deposition, but the greater part of embryonic development occurs during the 24 or 48 hours prior to hatching. The embryo emerges through an irregular break in the side of the shell.

The life histories of 108 amictic and 111 unfertilized mictic females were studied and compared in detail. These individuals were characterized by a high degree of genetic uniformity, since they were derived recently by parthenogenesis from a single common ancestor, and since they were derived from young mothers, less than 4 days old. This latter precaution eliminated the possibility of certain intrinsic differences, in fecundity, embryonic mortality and in the duration of certain periods in the life history, which result, in *Proales sordida* (Jennings and Lynch 1928–I, II), from differences in the ages of the parents.

The experimental females were cultivated individually under similar conditions, in small groups, during a period of two months. Uniformity of cultural conditions was obtained as follows. Small mass cultures, of 15 to 25 individuals in three drops of oat infusion, were maintained, the individuals being transferred daily to new fluid. Female-producing parthenogenetic eggs were removed from these cultures at the time of daily transfer, and isolated in depression slides, each one in three drops of oat infusion. The eggs isolated at any one time had thus been produced during the preceding 24 hours. The records of ages begin at the time of isolation, so that they are accurate only to a period of within 24 hours.

The eggs hatched as a rule during the first day after isolation. The young females grew rapidly and began to deposit eggs on the second day. Not until then could the individuals be recognized as mictic or amictic. They were transferred daily to clean slides and twenty-four hour infusion, at which time the number of eggs produced and other details were recorded for each mictic and amictic female.

Table I

Lecane inermis. Records of the numbers of eggs produced daily, throughout life, and of the total life duration, for typical contemporaneous amictic and unfertilized mictic females. *n. h.* signifies not hatched (on the first day); *d* signifies that the individual died on the day so marked.

Successive days of life		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total number of eggs	Length of life in days
Number of eggs laid by five amictic females	1	0	3	4	6	4	2	0d										19	7
	2	0	2	5	6	4	3	1d										21	7
	3	n.h.	1	4	5	6	(lost)												
	4	0	3	4	5	3	4	0d										19	7
	5	0	4	5	5	4	2	1	0d									21	8
Number of eggs laid by seven unfertilized mictic females	1	n.h.	1	4	4	4	3	0	0	0	0	0	0	0	0	0	0d	16	16
	2	0	3	4	4	3	0	0	0	0	0	0d						14	11
	3	0	3	4	5	3	0	0d										15	7
	4	0	3	4	4	4	1	0	0	0	0d							16	10
	5	0	2	3	4	4	3	0	0	0	0	0d						16	11
	6	1	4	4	3	2	0	0	0	0d								14	9
	7	1	4	4	4	3	0	0	0	0	0d							16	10

Since the male embryos require 30 hours or more for development, fertilization of the mothers by the sons was impossible, so that the mictic females as well as the amictic females reproduced throughout life only parthenogenetically.

During the two months of cultivation, the temperature varied from 19° to 24° C. Daily variations did not exceed one and one-half degrees. Although the mictic and amictic individuals were not distributed throughout this period in equal numbers, certain striking differences are observable in the life histories of the two kinds of females that cannot be attributed to differences in temperature, since they are exhibited by contemporaneous individuals subjected as nearly as possible to the same conditions of culture. Large contemporaneous cultures of the two types of females were at the time impracticable.

Table I gives the life histories with relation to the number of eggs produced daily, and the length of life, for two small groups of contemporaneous females of the two types. From Table I it is at once apparent that the mictic females (unfertilized) produce fewer eggs than the amictic females, but usually live longer. Further, on the whole, the egg-laying period of the mictic females terminates earlier.

Length of life and distribution of mortality

Table II gives for the individuals of the amictic and mictic populations the length of life in days (after their isolation as eggs); also the biometric constants, and the proportions that lived for the modal number of days, less than the mode and more than the mode.

As Table II shows, the largest number of individuals died, in both populations, on the ninth day, so that this is the modal length of life for both sets. But many of the mictic females (55.9 per cent) lived beyond this age, while fewer of the amictic females (32.4 per cent) did so. The maximum age reached by the amictic females was 15 days, while 13 per cent of the mictic females lived beyond this age, two reaching the ages of 27 and 28 days respectively. The mean length of life of the amictic females is 8.9 ± 0.11 days; of the mictic females, 11.0 ± 0.28 days. There are thus very characteristic and significant differences in the length of life reached by the amictic and mictic females respectively. Further, the duration of life is much more variable for the mictic than for the amictic females. For the amictic females the standard deviation in length of life is 1.72 ± 0.08 days, and the coefficient of variation is 19.28 ± 0.92 per cent, while for the mictic females the standard deviation is 4.37 ± 0.20 and the coefficient of variation 39.41 ± 2.04 per cent.

These differences in length of life are very noticeable in observation

Table II

Lecane inermis. Length of life in days (after their isolation as eggs) of amictic and unfertilized mictic females. The figures given in the body of the table are the numbers of individuals of each population that reach the ages in days indicated in the upper line of the table.

Days	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	Total
Number Amictic Females						7	20	15	31	16	12	5	1	0	1														108
Number Mictic Females					1	3	11	14	20	16	13	8	7	1	3	2	1	1	2	1	2	1	1	1	0	0	1	1	111

	Mean	Standard Deviation	Coefficient of Variability	Mode	Per cent below mode	Per cent at mode	Per cent above mode
Amictic Females	8.90 ± 0.11	1.72 ± 0.08	19.28 ± 0.92	9	38.88	28.70	32.41
Mictic Females	11.10 ± 0.28	4.37 ± 0.20	39.41 ± 2.04	9	26.13	18.02	55.86
Difference	− 2.20 ± 0.30	− 2.65 ± 0.21	− 20.13 ± 2.24	0	12.75	10.68	− 23.45

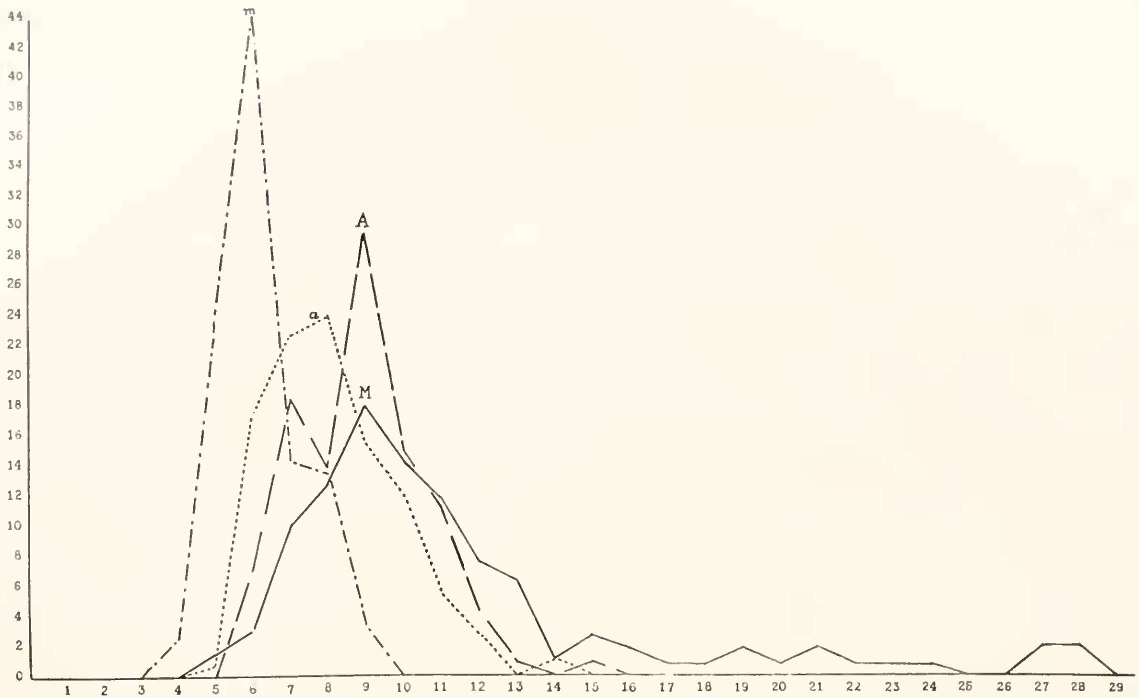

FIG. 9. *Lecane inermis.* Graphs showing the proportions of individuals reaching the different ages, in the amictic population (*A*), and in the population of unfertilized mictic females (*M*); also the ages at which the amictic females (*a*) and the unfertilized mictic females (*m*) cease egg-deposition. Age reckoned in days from time of isolation (within 24 hours after deposition). Horizontal scale, days of life; vertical scale, percentages of each population.

of the living animals. The mictic females cease egg-laying early in life, but most of the individuals continue to swim about actively for several days after, a few of them for many days. In these long-lived individuals physical decline is very gradual. The gastric glands and mastax become blackened and locomotion wanes, typical signs of structural degeneration. But the mictic females may linger on for many days in this condition. The amictic females, on the other hand, frequently show signs of age before the last egg is produced and all are dead within two days thereafter.

The distribution of mortality is represented graphically in Figs. 9 and 10. In Fig. 9, curves *M* and *A* show the proportions of the mictic and amictic populations respectively that reached the different ages. Figure 10 represents mictic and amictic individuals as though contemporaneous, and shows the proportions of each population present at the beginning of each day. Embryonic mortality is negligible; only one egg of the 220 eggs isolated failed to hatch. In this respect early-born mictic and amictic females resemble early-born populations of *Proales sordida* (Jennings and Lynch, 1928—II, Fig. 15). None die during immaturity; all live through the fourth day. All of the amictics and 99 per cent of the mictics survive the fifth day after isolation, that is, four days of fecundity. On every day thereafter, fewer amictic than mictic females are still alive. In both populations the mortality rate is low on the sixth day, higher on the next and reaches a maximum on the ninth day. It thereafter decreases until all the amictics are dead on the fifteenth day and the mictics linger on, two or three dying on successive days until the twenty-eighth day.

To what extent is the difference in longevity of the mictic and amictic females correlated with, or the result of, difference in fecundity? Information regarding this question is obtained from examination of the distribution of fecundity in the two populations, the rate of egg-production, the duration of the post-fecund period and the age at which the production of eggs ceases.

Fecundity

Inspection of Table I, giving the life history records for contemporaneous mictic and amictic females, has shown that the mictic female deposits only 14 to 16 of the small, male-producing eggs; the amictic female deposits 19 to 21 of the larger, female-producing eggs. Table III presents a comparison of the distribution of fecundity in the two populations, with the biometric constants; and Fig. 11 shows the proportions of individuals that produced the different numbers of eggs. The differences in the fecundity of the two types of female are striking. The amictic females produce 13 to 24 eggs per individual; the modal

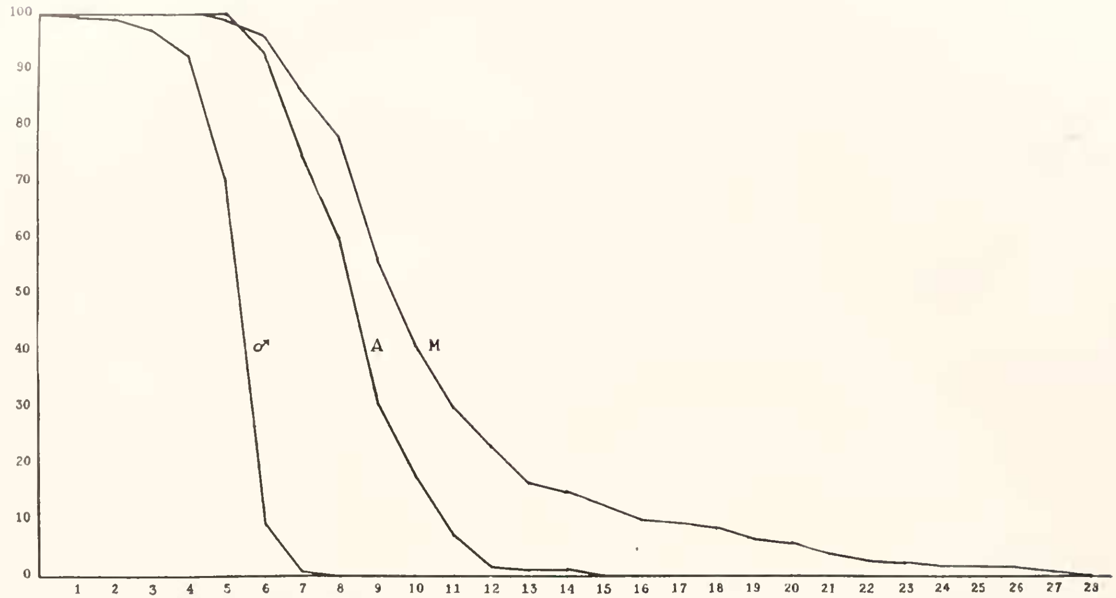

FIG. 10. *Lecane inermis.* Mortality and survivorship diagrams for the three different types of individuals, the amictic females (*A*), the unfertilized mictic females (*M*) and the males (♂). Horizontal scale, days of life; vertical scale, percentages of the populations surviving on the successive days.

TABLE III

Lecane inermis. Comparison of the fecundity of amictic and unfertilized mictic females. Total number of eggs produced during its life-time by each of the 111 mictic and 108 amictic females.

Number of eggs	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	Total
Number amictic females..........														1	0	1	3	3	5	11	18	27	17	16	6	108
Number mictic females...........			1	0	0	0	0	0	0	0	0	2	10	15	29	31	23									111

	Mean		Standard Deviation		Coefficient of Variability	
(*a*) Amictic Females (108)........	20.73	± 0.13	2.06	± 0.09	9.92	± 0.46
(*b*) Mictic Females (111)........	14.22	± 0.11	1.74	± 0.08	12.22	± 0.56
(*c*) Mictic Females, without individual that produced 2 eggs (110)....	14.33	± 0.08	1.29	± 0.06	9.03	± 0.41
Differences *a–b*........	6.51	± 0.17	0.32	± 0.12	− 2.30	± 0.73
a–c........	6.40	± 0.16	0.77	± 0.11	0.89	± 0.62

fecundity is 21 and the mean 20.7 ± 0.13. The mictic females produce 11 to 16 eggs (with the exception of one individual which produced only two eggs and died on the fifth day); the modal fecundity is 15, and the mean 14.2 ± 0.11. Thus, the mictic females produce regularly only two-thirds as many parthenogenetic eggs as the amictic females. The fact that the coefficients of variability for both populations are low, 9.9 per cent for the amictics and 12.2 per cent for the mictics, emphasizes the difference in the fecundity of the two types of females.

Excluding the single exceptional mictic female which produced only two eggs, the mean fecundity for the mictic population (110 individuals) is 14.3 ± 0.08, the standard deviation 1.29 ± 0.06, which is less than that of the amictic population by 0.77 ± 0.11, a significant difference, and the coefficient of variability is reduced to 9.03 ± 0.41, which is almost the same as that of the amictic females.

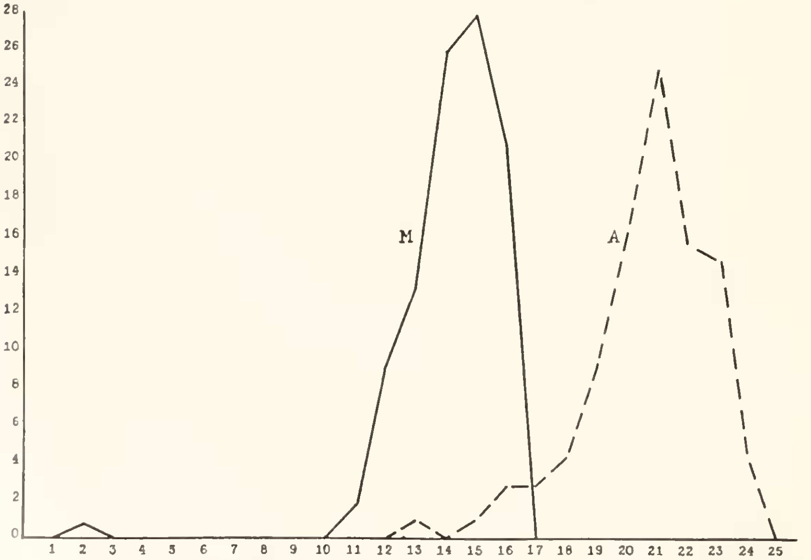

FIG. 11. *Lecane inermis.* Graphs showing the numbers of eggs produced by individuals of the two populations, the amictic females (*A*) and the unfertilized mictic females (*M*). Horizontal scale, numbers of eggs produced; vertical scale, percentages of the populations producing the different numbers of eggs.

The two populations differ further in the fact that a very much greater proportion of the mictic females produced the maximum or nearly the maximum number of eggs. This is clearly observable in Fig. 11. Whereas 48 per cent of the mictic females produced 15 or 16 eggs, only 21 per cent of the amictics produced 23 or 24 eggs. The mode and the mean fecundity more nearly coincide with the maximum in the mictic population.

Duration of the fecund period and rate of egg-production

It will be recalled that the mictic and amictic females mature and deposit the first eggs at about the same time, during the second day after isolation, also that the mictic female deposits but two-thirds as many eggs as the amictic female. If the male-producing parthenogenetic eggs are deposited at the same rate as the female-producing eggs, the fecund period of the mictic female should be only two-thirds as long as that of the amictic female.

TABLE IV

Lecane inermis. Duration of the period of fecundity of amictic and unfertilized mictic females. The figures given in the body of the table indicate the number of individuals in each population that required for the production of their eggs the number of days indicated on the upper line.

Number of days	2	3	4	5	6	7	8	9	10	11	Total
Number of Amictic Females..........			4	30	30	19	14	9	1	1	108
Number of Mictic Females...........	1	0	22	57	26	5					111

	Mean	Mode	Standard Deviation	Coefficient of Variability
(*a*) Amictic Females (108)....	6.42 ± 0.09	5, 6	1.44 ± 0.07	22.45 ± 1.08
(*b*) Mictic Females (111)......	5.10 ± 0.05	5	0.83 ± 0.04	16.22 ± 0.75
(*c*) Mictic Females, without individual that produced 2 eggs and died on 5th day (110)....................	5.13 ± 0.05		0.78 ± 0.04	15.13 ± 0.70
Differences *a–b*.............	1.32 ± 0.11		0.61 ± 0.08	6.23 ± 1.32
a–c.............	1.29 ± 0.10		0.66 ± 0.08	7.32 ± 1.29

In Table IV is given the number of days during which the females of both classes continue to produce eggs. The minimum number of days of the fecund period was the same for both (with the exception of the one individual, which produced only two eggs and died on the fifth day); but the total number of days ranged from 4 to 7 for the mictic females, from 4 to 11 for the amictic females. The mode for the mictics is five days; for the amictics 5 and 6 days are equally common. For 23 per cent of the amictics the period of fecundity exceeds the maximum period for the mictics. The mean for the mictics is 5.10 ± 0.05 days, for the amictics 6.42 ± 0.09 days. The standard deviation is, for the amictics 1.44 ± 0.07, for the mictics 0.83 ± 0.04. The coefficient of variability is, for the amictics 22.45

± 1.08, for the mictics, 16.22 ± 0.75. The differences in the mean, standard deviation and the coefficient of variability of the two populations are statistically significant, regardless of whether the one exceptional mictic female is included in the calculations (Table IV).

The mictic female requires on the average only one and three-tenths days less to produce its eggs, though these are fewer by one-third than the number produced by the amictic female. This means that, although both types of females produce 3 to 5 eggs per day, rarely 6, the mictic female deposits its small (male-producing) eggs, on the average, in less rapid succession than the amictic female deposits its larger (female-producing) eggs. The mictic female deposits, on the average, 3.8 eggs per day, or one every 8.6 hours; the amictic female 3.2 eggs per day, or one every 7.5 hours. These figures represent the quotients of the mean fecundity divided by the mean duration of the fecund period. Additional data regarding the rate of egg-deposition are given later in the paper.

Age at cessation of fecund period and duration of post-fecund period

In Table V is given the duration of the post-fecund period for all individuals of the two populations. Most of the amictic females (59 per cent) died within 24 to 36 hours after deposition of the last egg; 33 per cent died within one day, all died within two days thereafter.

TABLE V

Lecane inermis. Duration of the post-fecund period of amictic and unfertilized mictic females. Those individuals that produced eggs on the day on which they died, or as many as four eggs on the day preceding death are considered as having a post-fecund period of one day or less; if they produced no eggs on the last day, but one to three on the preceding day, they are listed as having a post-fecund period of one to one and one-half days; if they produced no eggs on the last two, three or four days, their post-fecund period is correspondingly two, three or four days, etc.

Number of Days	One day or less	1–1½	2	3	4	5	6	7	8	9	10
Number of Amictic Females..........	36	64	8								
Number of Mictic Females..........	2	15	20	18	17	6	11	2	2	3	3

Number of Days	11	12	13	14	15	16	17	18	19	20	21	22	Total
Number of Amictic Females...													108
Number of Mictic Females....	1	1	3	1	2	0	0	2	0	0	1	1	111

Not so with the mictic females. Only 33 per cent of the entire population died within two days after the cessation of egg-deposition.

Of these, 20 individuals survived for two days, 15 for one and one-half days, only two died within 24 hours after deposition of the last egg. While two days after the cessation of egg-production is the commonest period of death, three or four days are almost equally common; five and six days less frequent. A few individuals survive 7 to 22 days after the cessation of egg-production, there being, however, but one, two or three individuals in each class. Yet 20 per cent of the mictic females lived more than 6 days after the fecund period had ended.

As set forth in the preceding section, the mictic females cease to deposit eggs earlier, on the average, than the amictic females. The post-fecund period of the mictic females is thus extended in this way by about 1.3 days. However, this accounts for only a small fraction of the greater length of life of the mictic females after the cessation of egg-deposition. The mictic females have, on the whole, a much greater ability to survive the period of fecundity than the amictics.

This striking difference is shown for the entire populations in Fig. 9, representing the distribution of ages at the cessation of egg-production in comparison with the distribution of ages at death.

TABLE VI

Lecane inermis. Comparison of the ages at which amictic and unfertilized mictic females cease the deposition of eggs.

Age in Days	4	5	6	7	8	9	10	11	12	13	14	Total
Number of Amictic Females......	0	1	19	25	26	17	13	6	0	0	1	108
Number of Mictic Females........	3	24	49	16	15	4						111

Table VI gives for both populations the number of individuals that cease egg-production at the different ages. The fecund period of the amictic females terminates usually on the seventh and eighth days; that of the mictic females usually on the sixth day. As stated in a previous section, all of the amictic females and all but one mictic female live through four days of egg-production. Mortality then begins in both populations and rises to a maximum on the ninth day. Thus, the maximum mortality in the amictic population occurs from one to two days after the maximum number of individuals cease egg-production; in the mictic population, three or four days thereafter. After the ninth day, the distribution of mortality of the amictic females follows the cessation of egg-production within one or two days. The mictic females, however, have all ceased egg-production at the end of the ninth day, and 56 per cent are still alive. These die at a slow rate until the 14th day, the remaining 15 per cent at a fairly uniform rate until the 28th day.

Relation of length of life to fecundity and rate of egg-production

The foregoing data indicate that the difference in the length of life of mictic and amictic females results, in part, from the difference in their ability to survive the fecund period. This has been evidenced by the relative duration, in the two populations, of the fecund and post-fecund periods, and the relative ages at which egg-production ceases.

We may inquire further into the extent of the relationship between length of life and fecundity of mictic and amictic females, by comparing the fecundity, rate of egg-production, and the duration of the post-fecund period, in relatively short-lived, average-lived and long-lived individuals of each population. Those that lived less than 9 days, the mode, are classified arbitrarily as short-lived, those that lived 9 days as average-lived and those that lived more than 9 days as long-lived. The results of this comparison are presented in Tables VII to IX.

TABLE VII

Lecane inermis. Comparison of the relation of life duration to fecundity displayed by amictic and unfertilized mictic females. Individuals that lived less than 9 days, the mode, are called short-lived; those that lived 9 days are called average-lived, and those that lived more than 9 days, long-lived.

		Short-lived	Average-lived	Long-lived		Total
				Total	Those living beyond 15 days	
Amictic Females	Number	42	31	35	0	108
	Mean eggs	19.95	20.45	21.91		
Mictic Females	Number	29	20	62	14	111
	Mean eggs	14.0	14.05	14.2	14.64	

Table VII gives the mean fecundity for these groups. The short-lived amictic females produced, on the average, 19.95 eggs per individual, the average-lived 20.45, the long-lived 21.91. The difference in the mean fecundity of short-lived and long-lived amictic females is 1.96 eggs. The short-lived mictic females produced, on the average, 14.0 eggs per individual, the average-lived 14.05, the long-lived 14.2. The difference in the mean fecundity of short-lived and long-lived mictic females is 0.2 eggs, which is only one tenth of the difference (1.96) found in the corresponding groups of amictic females. The mean fecundity of those mictic females that lived beyond 15 days, and thus survived all the amictic females, is 14.6 eggs; that is, it is greater than the mean fecundity of short-lived mictic females by only 0.6 eggs. The positive correlation between length of life and the number of eggs produced is appreciably more marked for the amictic females.

TABLE VIII

Lecane inermis. Comparison of the relation of life duration to rate of egg-deposition (number of eggs per day) for amictic and unfertilized mictic females. The "mean rate" of egg-deposition is the average of the rates at which all the members of a particular group deposited their eggs. The rate of egg-deposition of each individual is computed by dividing the total number of eggs produced, by the number of days on which eggs were deposited by that individual.

		Short-lived	Average-lived	Long-lived		Total
				Total	Those living beyond 15 days	
Amictic Females	Number	42	31	35	0	108
	Mean rate	3.88	3.33	2.73		
Mictic Females	Number	29	20	62	14	111
	Mean rate	3.0	2.78	2.78	2.87	

The length of life of the amictic females bears a negative correlation with the rate at which they produce their eggs (Table VIII). The short-lived individuals are found to have deposited their eggs in more rapid succession than individuals that lived 9 days or longer. They deposited, on the average, 3.9 eggs per day, the average-lived 3.3 eggs per day, the longer-lived 2.7 eggs per day. The short-lived mictic females deposited 3 eggs per day, the average-lived 2.8, the long-lived also 2.8 eggs per day. Those in the latter group that lived 16 days or more deposited, on the average, 2.9 eggs per day. The length of life of the mictic females apparently bears little relation to the rate at which their eggs are deposited.

It should be noted also that each group of mictic females is characterized by an average daily egg-production almost the same (within 0.3 eggs) as the group of amictic females that produced their eggs most slowly, namely, the long-lived individuals. The amictic group with the highest rate of egg-deposition (the short-lived individuals) produce, on the average, 0.9 eggs per day more than the corresponding group of mictic females. These facts confirm and supplement data given in a previous section which indicate that the mictic female produces its eggs more slowly than the amictic female.

We find, furthermore (Table IX), in the amictic population, that whereas 25 (60 per cent) of the short-lived individuals died within 24

Table IX

Lecane inermis. Comparison of the relation of length of life to the duration of the post-fecund period for amictic and unfertilized mictic females. The figures in the body of the table indicate the number of individuals that survived after the cessation of egg-production for the number of days indicated on the upper line.

Number of Days		1 or less	1 to $1\frac{1}{2}$	2	3	4	5	6	7	8	9–22	Total
Short-lived Females	Amictic	25	16	1								42
	Mictic	2	9	14	4							29
Average-lived Females	Amictic	6	22	3								31
	Mictic		5	2	8	5						20
Long-lived Females	Amictic	5	26	4								35
	Mictic		1	4	6	12	6	11	2	2	18	62
Total number	Amictic											108
	Mictic											111

hours after deposition of the last egg, only 6 (19 per cent) of the average-lived and 5 (14 per cent) of the long-lived died within this period. Twenty-two (71 per cent) of the average-lived and 26 (74 per cent) of the long-lived females survived for 24 to 36 hours after deposition of the last egg. Only 8 individuals (7 per cent of the entire population) survived as long as two days after the cessation of egg-production.

However, all of the mictic females, with the exception of two short-lived individuals, lived more than 24 hours after the cessation of egg-production. Most of the short-lived mictic females survived one and one-half or two days. The average-lived survived usually three days, though one and one-half and three days were almost equally common. The long-lived individuals, which constitute 56 per cent of the population, survived one and one-half to 22 days after the cessation of egg-production, commonly 4 to 6 days. Only 10 per cent survived less than 4 days; 20 per cent survived longer than 6 days.

In short, the amictic females that lived for less than 9 days produced their eggs, on the average, in more rapid succession than those that lived longer; they also produced fewer eggs and died usually within 24 hours after deposition of the last egg. These facts suggest that rapid rate of egg-production exhausts the short-lived amictic females, rendering them incapable of completing the transformation of their germ cells into eggs, thus reducing their fecundity. So strenuous is the fecund period that none is able to survive more than two days after its cessation.

In the mictic population, as in the amictic population, the longest-lived individuals are those that have, on the average, produced their eggs more slowly, have produced a larger number of eggs and have survived more than a day after the deposition of the last egg. However, the length of life of the mictic female is correlated in less degree than that of the amictic female with the number of eggs produced and the rate at which they are produced. The short-lived mictic females usually survive as long after the cessation of egg-deposition as the longest-lived amictic females; they very infrequently show signs of physical exhaustion before the completion of egg-production. We may conclude, then, that the greater longevity of the mictic females, which involves a greater ability to survive the fecund period, results, in part at least, from the fact that for them the process of egg-production is less strenuous. This is to be expected in view of the fact that they produce fewer, smaller eggs at a less rapid rate than the amictic females.

General and comparative

Under similar conditions of cultivation amictic and unfertilized mictic females of *Lecane inermis* differ markedly in length of life, fecundity, rate of egg-production, duration of the fecund and post-fecund periods and in the degree of correlation between fecundity and length of life. How are these differences between the two types of females produced?

In their investigation of the diversities that arise within a clone of (amictic) females of the parthenogenetic rotifer, *Proales sordida*, Jennings and Lynch (1928) concluded that differences in length of life, among those individuals that hatch, are not an expression of intrinsic diversity. They result, rather, from the accidents of life, the interaction of the rhythmic processes of digestion and reproduction, combined with disturbances in these processes imposed by the daily transfer of the individuals to clean slides.

In *Lecane inermis*, the difference in the length of life of the mictic and amictic female results largely from the difference in the severity of the process of egg-production, hence in their ability to survive the fecund period. Both mictic and amictic females lived most commonly nine days, but many more mictic than amictic females lived beyond this age, presumably because they produce fewer, smaller eggs than the amictic female, at a slower rate, and cease egg-deposition at an earlier age. Thus, in *Lecane inermis*, differences in length of life are probably to be considered of an intrinsic nature only in so far as they result from intrinsic differences in fecundity.

The mictic females of *Lecane inermis* resemble the females of *Proales sordida* in that some of them are able to live for many days after the cessation of egg-production. The amictic females of *Lecane inermis*, however, never survive more than 3 or 4 days thereafter. Both mictic and amictic females differ from *Proales sordida* in the degree of correlation between length of life and fecundity. For individuals of *Proales sordida* that live entirely through the period of fecundity (24 hours after deposition of the last egg) there is no correlation between length of life and the number of eggs produced; longer-lived individuals have, on the whole, produced neither fewer nor more offspring than the average (Jennings and Lynch, 1928—II, p. 371). In *Lecane inermis*, on the other hand, among those individuals that lived entirely through the fecund period, the longer-lived amictic females and those mictic females that lived for more than 15 days have a somewhat greater average fecundity than those that lived a shorter time.

What is the origin of the difference in fecundity which is, in *Lecane inermis*, largely responsible for the difference in longevity of the mictic and amictic female? In *Proales sordida*, intrinsic diversities in fecundity arise among the individuals of a clone in correlation with the size of the eggs from which they have hatched. Smaller (usually early-born) eggs produce less fecund individuals than larger (later-born) eggs. In order to eliminate diversities that might arise in this way, only early-born individuals were used in the present investigation. Although measurements have not been made, there is no observable difference in the size of the parthenogenetic eggs that produce the two different kinds of females of *Lecane inermis*. In the viviparous species *Asplanchna intermedia*, on the other hand, the mictic female is apparently derived from a smaller embryo and is less fecund than the amictic female (Tauson, 1925, p. 144).

As Jennings and Lynch point out (with respect to *Proales sordida*), differences in fecundity must proceed either from differences in the ability of the individuals to transform their germ cells into eggs under the conditions of cultivation employed, or from differences in the original number of their germ cells. There is (as they observe) evidence that the number of germ cells, as well as of the other cells of the body of rotifers, is fixed during the embryonic period. Cell mitoses are not observed later in life. Nachtwey (1925) has shown that the rotifer *Asplanchna priodonta* has usually 32 germ cells, derived by five cell cleavages from the single primitive germ cell. In view of this evidence, Jennings and Lynch (1928—I) have suggested that differences in the fecundity of the (amictic) females of *Proales sordida* that are derived from smaller eggs and those derived from larger eggs may result from differences in the original number of germ cells. Late-born individuals may have usually 32 germ cells, early-born individuals a smaller number, resulting from failure of a portion of the fourth cell generation to undergo another division.

In *Lecane inermis* the observed difference in the fecundity of the two types of female would result if the primitive germ cell of the mictic female undergoes regularly only four successive divisions, producing 16 oöcytes; and if, in the amictic female, one-half of the fourth cell generation regularly proceeds to a fifth cleavage, thus producing 24 germ cells. Cytological investigation would, of course, be required in order to determine whether there exists a difference in the original number of germ cells.

It is possible that, under conditions other than those of this investigation, the mictic female might be able to bring to maturity as many germ cells as the amictic female. It should be noted, however, that the differences in the fecundity and length of life of the two types of females have been observed during cultivation under widely different conditions; namely, in oat infusion and in Benecke solution at temperatures ranging from 18° to 24° C.

The observations of Whitney (1907) regarding the fecundity of mictic and amictic females of *Hydatina senta* are of interest here. At 20° to 22° C. both types of females produce about the same number of eggs; at 24°–26° C. the mictic female produces twice as many eggs as the amictic; at 26°–29° C. the mictic female produces four times as many eggs as the amictic female. Thus, in *Hydatina senta*, differences in the fecundity of the two types of female result observably from differences in response to the environment. The mictic female lives at all these temperatures slightly longer than the amictic female (Wesenberg-Lund, 1929). The relative longevity of the amictic and mictic female of *Hydatina senta* is not correlated with the relative fecundity, as in *Lecane inermis*.

For other species, information regarding the relative length of life, fecundity and rate of egg-production of the mictic and amictic female is not extensive.

The life history records of three mictic females of *Euchlanis triquetra* (Lehmensick, 1926) indicate that they produce the same number of eggs as the amictic female (24) and live about the same length of time, 21 days. But the mictic female produces its eggs more rapidly and thus lives longer after the cessation of egg-production.

The mictic female of *Asplanchna intermedia* (Tauson, 1925) produces fewer eggs, as mentioned above, and lives a shorter length of time than the amictic female. The mictic female matures on the first day, produces 10 to 12 eggs on the second day, which hatch on the third day; the mother dies after the hatching of the last male. The amictic female lives 5 or 6 days, produces daily no more than 4 eggs (probably 16 to 20 in all). The mictic female produces its eggs appreciably more rapidly.

In *Pterodina elliptica* (Luntz, 1926), the mictic female produces regularly six or seven eggs, the amictic female only five. There is no available information regarding the length of life. Physiological diversity is manifested by the inability of the mictic female to withstand certain conditions of osmotic pressure and pH in which the amictic female is perfectly normal.

Wesenberg-Lund states (1930, p. 31) that "if not fertilized, investigations hitherto carried out seem to show that the number of eggs laid by the two sorts of females is almost the same, but that those of the mictic female are laid in a much shorter time (Lehmensick, 1926, *Euchlanis triquetra*)."

We find, however, that the mictic females of some species, *e.g.*, *Asplanchna intermedia* and *Lecane inermis*, are regularly less fecund than the amictic females, whereas those of some other species, *e.g.*, *Pterodina elliptica* and *Hydatina senta* are, usually, more fecund. With regard to the relative rates at which the eggs are deposited by the two sorts of females, *Lecane inermis* is exceptional; the mictic female produces its eggs less rapidly than the amictic female.

Wesenberg-Lund (1930) presents a comparison of the mictic and amictic females on the basis of his extensive investigations carried out largely in nature, but supplemented by laboratory observations. The author stresses the physiological and biological differences between the mictic and amictic female and gives some additional data regarding their relative fecundity, rate of egg-production and length of life. In *Asplanchna sieboldi* the mictic females mature and begin to deposit eggs earlier than the amictic females. In isolation cultures they produced 14 to 16 eggs and lived 10 to 12 days. Amictic females, in mass cultures, lived only 8 days and produced 8 to 10 eggs. The author is inclined to believe (p. 156) that in nature the amictic females live longer than the mictics, especially at low temperatures. Concerning *A. brightwelli* he "conjectures that at the same temperatures the amictic females live some days longer than the mictic ones;

produce more young ones; and to a somewhat higher degree are able to accommodate duration of life and time of production of young ones to temperature" (p. 149). Regarding the rate of production of the parthenogenetic eggs, Wesenberg-Lund states (p. 210) that, in several species, "the mictic female is able to subdivide the yolk mass into small amounts, and produce about 12 eggs simultaneously, whereas the amictic females produce the eggs successively." Further evidence of physiological diversity is presented by certain parasitic species in which the amictic females are usually free-living, the mictic females always parasitic. Peculiarities in behavior exhibited by mictic females of some species after fertilization indicate that they are structurally as well as physiologically diverse.

In summary, the evidence at hand is sufficient to demonstrate that in different species the relative fecundity, length of life and rate of egg-production of the mictic and amictic female vary greatly. In every species which has been studied physiological differences between the two types of female are demonstrable; but investigations have not proceeded sufficiently far to admit of general conclusions regarding the nature of the fundamental diversity that distinguishes the mictic from the amictic female.

Fertilized Mictic Females

In the foregoing only unfertilized mictic females have been considered. The mictic female of *Lecane inermis*, like that of *Pterodina elliptica* and *Brachionus bakeri* (Luntz, 1926, 1929), and *Asplanchna sieboldi* (Wesenberg-Lund, 1930, p. 155), may be fertilized during its immature period or after having deposited parthenogenetic eggs. In some species the mictic female can be fertilized only when very young (*Euchlanis triquetra*, Lehmensick, 1926).

The mictic females of *Lecane inermis* resemble those of most species in that they may be fertilized by their own sons. The females of *Pterodina elliptica* are exceptional in that they are incapable of being fertilized by the male progeny of the same grandmother. In *Lecane inermis* cloacal copulation occurs. The toes of both male and female are bent ventrally, almost at right angles to the axis of the bodies, which are extended in opposite directions. The female continues to swim about, pulling the male along with her. Copulation lasts for at least five to ten minutes. The cloacal method of copulation is uncommon in rotifers, according to Wesenberg-Lund (1929). The males of most species attach themselves to the body of the female and in some manner pierce the body wall and deposit sperm directly in the body cavity.

As noted by all investigators of the bisexual rotifers, fertilization produces a visible effect upon the vitellarium. This organ becomes black during the growth of the fertilized egg. This, it is generally believed, results from the deposition of fat and the production of larger, darker yolk granules. In the course of 24 to 36 hours a fertilized egg matures and is deposited. The vitellarium is then quite colorless. The production of yolk and the deposition of a fertilized egg may be repeated four or five times.

Information regarding the fecundity and length of life of fertilized mictic females of this species is derived from the life history records of 18 individuals fertilized during immaturity and 5 individuals fertilized by their own sons. The individuals fertilized before maturity produced only fertilized eggs, the total number not exceeding five. They lived usually 4 or 5 days after the cessation of egg-production; the total length of life ranged from 10 to 25 days.

The life history records of the five females fertilized by their own sons at various times during maturity are given in Table X. These individuals produced 5 to 9 parthenogenetic eggs before being fertilized. They produced thereafter one to 4 fertilized eggs. They are typical in their ability to survive the fecund period. The total length of life ranged from 13 to 18 days.

Mictic females of this species have not been observed to deposit parthenogenetic eggs after once having produced fertilized eggs. This is not the case in *Hydatina senta* (Shull, 1910) and in several other species. Lehmensick (1926) suggested that fertilized mictic females return to the production of parthenogenetic eggs because all of their germ cells were not fertilized at the first mating, and Wesenberg-Lund has observed that after a second mating the production of fertilized eggs may be resumed (1930—II, p. 154). The failure of fertilized mictic females of *Lecane inermis* to produce parthenogenetic eggs probably indicates that more of their germ cells were fertilized than they were capable of bringing to maturity; for, frequently, after the cessation of egg-deposition the vitellaria contained dark yolk granules and fertilized eggs were present in various stages of growth.

Fertilization commonly reduces the fecundity of the mictic female. *Lecane inermis*, which produces, when fertilized, only 5 to 10 eggs rather than 16, is not exceptional in this respect. The length of life is, in this species, apparently not affected by fertilization.

The Males

The males of this species (Figs. 4 and 5) are strikingly different in appearance from the females, and, like most male rotifers, are to

Table X

Lecane inermis. Records of the numbers of male-producing and fertilized eggs produced daily, throughout life, and of the total life duration of five mictic females, fertilized at various times during the fecund period. The numbers given in the body of the table are the numbers of eggs deposited, on the days indicated on the upper line, by each of the five individuals. The designation (♂) below the numbers indicates male-producing eggs; numbers not so marked indicate fertilized eggs.

Individuals	Days of Life																		Fecundity			Life in days
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	Male eggs	Fertilized eggs	Total	
1	0	5 ♂	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0d	5	2	7	18
2	0	0	2 ♂	3 ♂	2· ♂	0	1	1	1	1	0	0	0d						7	4	11	13
3	0	0	3 ♂	3 ♂	2 ♂	1 ♂	1	0	0	0	0	0	0	0	0	0	0	0d	9	1	10	18
4	0	1 ♂	3 ♂	3 ♂	1 ♂	1	1	0	0	0	0	0	0	0	0	0	0d		8	2	10	17
5	0	1 ♂	2 ♂	2 ♂	1 ♂	1	1	1	0	0	0	0	0	0d					6	3	9	14

some extent degenerate in structure. The females are somewhat flask-shaped, flattened dorso-ventrally, and become pigmented as they age. The males, on the other hand, are nearly cylindrical, transparent, and are somewhat shorter and about one-half the width of the newly-hatched female. The toes of the female are long and slim, those of the male are short and thick. The lorica of the male, especially in the posterior region, shows a greater degree of segmentation than that of the female, and the body is thus more flexible. One of the most striking peculiarities of the male rotifer is a black, disk-shaped body. It consists of a vesicle containing large, dark granules, which are supposed by Leydig to be excretory in nature (Wesenberg-Lund, 1929, p. 327). This structure is located dorsally in the posterior region of the body.

The females more than double their size through growth (compare Figs. 2 and 3); the males do not grow. This lack of the power of growth is characteristic of the males of most species of rotifers and is associated with the absence of a functional digestive system. In *Lecane inermis*, no traces of the mastax and digestive glands, so prominent in the female, have been observed in the male. Apparently, only the rudimentary anterior portion of the digestive tube persists, and this serves, as in other species (Wesenberg-Lund, 1923, 1929), as a suspensor ligament for the testis (compare Figs. 3 and 5).

The excretory system shows some structural reduction in the absence of the contractile vacuole.

The reproductive system is well-developed. The testis is large and fills most of the body cavity. The vas deferens is also conspicuous. Two large bodies lying ventral to the testis and vas deferens may be the so-called prostate glands, two or four of which are usually present in the male rotifers. The structure and method of functioning of the copulatory organ has not been observed.

A prominent retro-cerebral organ and eye-spot are present, as in the female. The activity and flexibility of the male indicate well-developed nervous system and musculature.

The males hatch from the small eggs of the mictic female after a developmental period somewhat exceeding in duration that of the females. Four male parthenogenetic eggs, allowed to develop in standard oat infusion at 23° C., required two hours longer to develop than four female parthenogenetic eggs laid at the same time and subjected to identical conditions during development. The average time required by the male eggs was 31 hours 16 minutes, by the female eggs 29 hours 45 minutes, a difference of one hour and 31 minutes. In a suspension of *Chlorella* and *B. proteus* in Benecke solution of

0.07 per cent concentration, at 22°–24° C., the male embryos require on the average four hours longer for hatching than the female embryos. The duration of the embryonic periods of male and female parthenogenetic eggs deposited by young parents and allowed to develop at the same time are given in Table XI.

TABLE XI

Lecane inermis. Comparison of the duration of the embryonic periods of contemporaneous male and female parthenogenetic eggs, deposited by young mothers, and allowed to develop at 22° to 24° C. The eggs were isolated in pairs on hollow-ground slides, usually a single male and female egg in each depression, in a suspension of *Chlorella vulgaris* and *B. proteus* in Benecke solution of 0.07 per cent concentration.

Number of hours after deposition	Number of contemporaneous eggs hatched	
	Female	Male
30	18	0
32	6	0
34	1	7
36	1	10
38	0	9
39—or longer	0	6
	Total 26	32

Male rotifers have been reported to be sexually mature at the time of hatching or shortly thereafter. This is true also of the males of *Lecane inermis.* During the first few days they are extremely active. They copulate indiscriminately with fertilized or unfertilized mictic females, or with the amictic females. This seems to be generally characteristic of rotifer males. The duration of sexual activity has not been investigated.

The males that hatch live usually 4 to 6 days. They are very active. They swim dorsal side up, commonly in a less direct path, and rotate less than do the females. The males of this species are also typical in the lack of the power of growth. On the fourth or fifth day, activity begins to wane until locomotion ceases entirely. The organism lies on its side in a semi-contracted condition, the anterior portion bent ventrally. This condition culminates in death usually within 24 hours.

For investigation of the length of life and rate of mortality, male eggs were isolated within 24 hours after deposition, from small mass cultures during a period of three weeks. These individuals, as well as the mictic and amictic populations previously described, belonged to the same pure line (descendants by parthenogenesis of a single stem mother). Of the 110 eggs isolated, 6 individuals that hatched were lost in transferring, and 22 (20 per cent) failed to hatch. Nine of those that failed to hatch were discarded before it was discovered that in many cases the embryos developed completely and were very active within the shell. Only one of the remaining 13 failed to develop. The other 12 individuals lived and were active the usual length of time within the shell; two lived longer than any of those that hatched.

Table XII

Lecane inermis. Length of life of 95 males, including 13 which developed but failed to hatch. The length of life is reckoned from the time of isolation of the eggs (within 24 hours after deposition). For comparison of the males with the females, the differences in the biometric constants of the different populations are given at the end of the table. The biometric constants for the female populations are given in Table II.

Number of days	1	2	3	4	5	6	7	8	Total
Those that hatched	0	1	1	4	20	50	6	0	82
Those that developed but failed to hatch	1	0	0	0	1	7	2	2	13

	Mean	Standard Deviation	Coefficient of Variability
Total studied (95)	5.69 ± 0.07	1.10 ± 0.05	17.48 ± 0.88
Total hatched (82)	5.65 ± 0.06	0.83 ± 0.04	14.73 ± 0.79
Difference between Males and Females			
Amictics (108)—Males (95)	3.21 ± 0.13	0.72 ± 0.09	1.80 ± 1.27
Mictics (111)—Males (95)	5.41 ± 0.29	3.37 ± 0.21	21.93 ± 2.22

Table XII shows the life duration of those males, hatched and not hatched (95 individuals), for which records are complete. They lived from one to 8 days. Sixty per cent of the population died on the sixth day, which was the modal length of life. Twenty-two per cent died on the fifth day and only a very few on any other day. The mean length of life of those that hatched is 5.65 days; including those that failed to hatch the mean is 5.69 days. The males live three days less than the amictic females, five and one-half days less than the mictic females. The standard deviation is significantly lower than that of both types of females; the coefficient of variability is only slightly less than that of the amictic females, but less than that of the mictic females by 22 per cent.

In Fig. 10, the rate of mortality of male and female populations is compared. Those that developed but failed to hatch are included in the graph. The rate of mortality increases very gradually until the fourth day, at the end of which seven and one-half per cent of the males, but no females are dead. During the fifth and the sixth days, 88 per cent of the male population die, while mortality is just beginning in the female population. All of the males are dead one day before mortality reaches its height in the female population.

The male and female populations differ in hatchability, in the mode and mean length of life, and in the standard deviation; but in the variability of life duration the males and the amictic females do not differ appreciably.

Is the difference in hatchability of the male-producing and female-producing eggs due to an inherent difference in fertility of the mictic and amictic females, or to differences in the ages of the parents or to the conditions of cultivation? The males were, for the most part (77 per cent), derived from females under four days old; all the females studied were deposited by individuals less than four days old. Most of the male-producing eggs that failed to hatch were derived from parents more than four days old, but six were early-born. Thus, 7 per cent of the early-born males and only 0.5 per cent (one in 220) of the early-born females failed to hatch. The female embryos that fail to hatch never live more than one or two days. Since the female and male populations were not cultivated at the same time, however, the failure of male embryos to hatch may have resulted from some environmental difference, and cannot be regarded as conclusive evidence that mictic females produce parthenogenetic eggs that are regularly less fertile than those from amictic females. Information regarding the relative fertility of the parthenogenetic eggs from mictic and amictic females is not available in the literature, in so far as I am aware.

The uniformly short length of life of the males in comparison with that of the females has been observed in other lines investigated on a smaller scale, in which, however, both sexes were cultivated at the same time.

The males of *Lecane inermis* live longer than the males of most other species hitherto described (Wesenberg-Lund, 1930, p. 158). The large males of the viviparous *Asplanchna* species live four or five days. The moderate reduction in length of life, in comparison with that of the females, is, in *Lecane inermis*, in accord with the moderate degree of structural degeneracy. Differences in the degree of structural degeneracy of the males of different species may bear some correlation with differences in the degree of reduction in the size of the male-producing parthenogenetic eggs and in the rate at which the eggs mature and are deposited, two factors which Wesenberg-Lund (1930) considers to be largely responsible for the structural degeneracy of the male rotifers. Evidence in support of this view is derived from a comparison of the males of *Lecane inermis* with those of the plankton rotifers. The former, which are characterized by a moderate degree of structural degeneracy and of reduction in length of life, are derived from eggs which are appreciably smaller than the female-producing eggs, but which are deposited less rapidly, and require a longer time for development. The males of the plankton rotifers, on the other hand, are derived from very small eggs, a large number of which, according to Wesenberg-Lund, are produced almost simultaneously, and develop rapidly. These males are small, consist of little more than reproductive system and live (in some cases) only a few hours. It should be borne in mind, however, that the tendency toward structural degeneracy and reduced vigor of the male rotifers may result from the haploid condition of their chromosomes (Morgan, 1926, Chapter X). The knowledge regarding these matters is at present very meager.

Summary

This paper is the first contribution of a series dealing with the life cycle of the bisexual rotifer *Lecane inermis* Bryce. The three types of individuals, the mictic females, the amictic females and the males, and the eggs from which they are derived, are described and their life histories are compared statistically. The individuals studied are intrinsically uniform members of the same genetic stock, cultivated under uniform environmental conditions, although they were not all contemporaneous. The comparison is based upon about 100 representatives of each type of individual.

The three types of individuals are characteristically different in length of life. The mean length of life is, for the amictic females, 8.9 ± 0.11 days, for the mictic females, 11.1 ± 0.28 days, for the males, 5.7 ± 0.07 days. This difference is apparent in their life curves. Embryonic mortality is negligible in all three populations. Mortality increases gradually in the male population until the fourth

day, then increases suddenly, 83 per cent of the population dying on the fourth to the sixth days. All are dead by the eighth day. All the females survive through the fourth day; thereafter the rate of mortality increases more rapidly in the amictic population. More than half of the mictic females survive the modal life duration, which is the same for both kinds; 12 per cent to 15 per cent survive the longest-lived amictic female and die off very gradually until the twenty-eighth day. The short life duration of the males is undoubtedly correlated with the structural degeneracy, especially of their digestive and excretory systems.

The longer life of the mictic females, as compared with the amictic females, results, in part at least, from the fact that egg-production is for them a less strenuous process. This is evidenced by the following facts. (1) Their male-producing eggs are smaller. (2) The mictic female produces regularly only two-thirds as many eggs as the amictic female. The maximum number is, for the mictic female, 16, exceptionally 17, for the amictic female 24. The mean number of eggs per individual is, for the mictic female 14.2 $\pm$ 0.11, for the amictic female, 20.7 $\pm$ 0.13. A higher proportion of mictic females produce their maximum number of eggs. The difference between the mode and the maximum is, for the mictics, only one, for the amictics, three. (3) The mean duration of the period of fecundity of the amictic female is 6.4 $\pm$ 0.09 days, with a standard deviation of 1.44 $\pm$ 0.07 and a coefficient of variability of 22.5 per cent; the mean for the mictic female is 5.1 $\pm$ 0.05 days, the standard deviation 0.83 $\pm$ 0.04, the coefficient of variability 16.2 $\pm$ 0.75 per cent. (4) During this time the mictic female deposits, on the average, one egg every 8.6 hours, the amictic female deposits one egg every 7.5 hours. (5) The amictic females die usually within 24 to 36 hours after deposition of the last egg; 19 per cent of the mictics lived more than six days thereafter. In summary, the mictic female produces in less rapid succession only two-thirds as many eggs as the amictic female, requires for the production of her eggs 1.3 days less than the amictic female and usually lives longer after the cessation of egg-production.

A comparison was made, for the mictic and amictic females, of the degree of correlation between length of life and their fecundity, rate of egg-production and ability to survive the fecund period. Short-lived amictic females are found to have produced fewer eggs than long-lived individuals, in more rapid succession, and to have died within a few hours after the deposition of the last egg, apparently exhausted by the severity of the process of egg-production. The length of life of the mictic female is correlated only in slight degree with the number of eggs produced and the rate at which they are produced.

The mictic female of this species may be fertilized during immaturity or after having produced parthenogenetic eggs. The fecundity of the mictic female is reduced by fertilization, the total number of eggs per individual, in 18 cases studied, not exceeding ten. The maximum number of fertilized eggs produced by a single individual was five. The length of life of the mictic female is not appreciably altered by the production of fertilized eggs.

The differences cited above are evidence of fundamental physiological diversity between mictic and amictic females and males of *Lecane inermis.*

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